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THE ANGULATION OF THE LIMBS OF PROBOSCIDIA, DINOCERATA, AND OTHER QUADRUPEDS, IN ADAPTATION TO WEIGHT.

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WITH material which in most cases belongs to several individuals the reconstruction of an extinct animal requires the greatest care and skill. When the proportions are determined the work is merely begun, for delicate calculation is needed to give the spine its proper curvature, to place the head in its true position, and then to give the bones of the fore and hind limbs their natural angles with each other. The angulation is most important because it finally determines the elevation of the body of the animal above the ground. Few of the mounted skeletons in our museums have the limbs correctly placed, and the drawings of skeletons, even in the best works, are often at fault in this respect.

Professor Marsh's statement in his monograph upon the Dinocerata, that in my restoration of Loxolophodon published in 1881, "the bones of the fore limb are in a position impossible in life," led me some years ago to study the means of ascertaining the position and angulation of the limbs in fossil quadrupeds, and especially of the fore limb. Professor Marsh's criticism refers to the fact that, in the restoration referred to, the humerus is only slightly bent backwards, and this does not indicate sufficient flexure at the elbow.

In cases of this kind our material for study lies in the articular surfaces of the fossil limb bones and a comparison of these surfaces with those in the nearest allied living types. My ground for restoring the limbs of Loxolophodon was the close likeness which exists between the articular surfaces and shafts of the humerus and radius and ulna of this type and those of the elephant.

In order to test the force of Professor Marsh's criticism and to guard against what might be a misleading resemblance, full-sized vertical sections were made of the fore limbs of *Uintatherium* (*Loxolophodon*) *cornutum* and of *Elephas indicus* in the Princeton collection. A section of a rhinoceros fore limb was also made for comparison. These were reduced by photography to a scale of 1 in 18 and are copied in Figs. 1, 2, and 3.

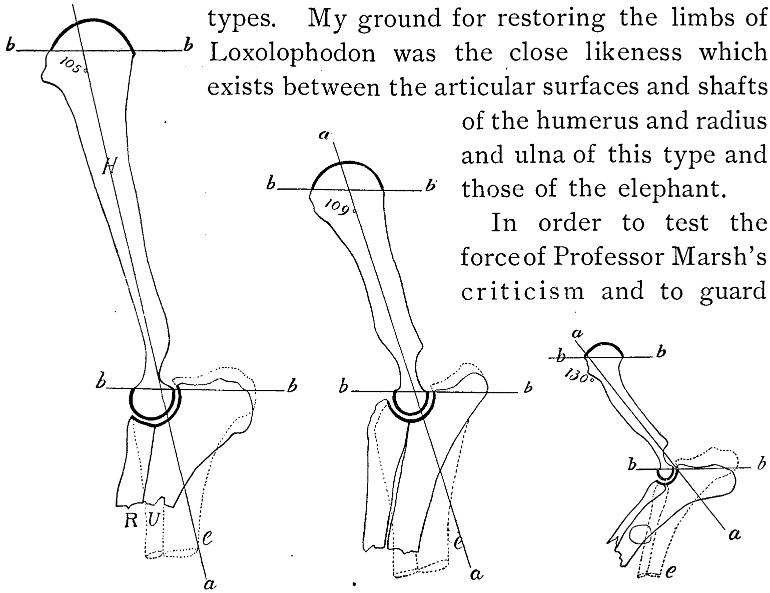

FIG. 1. FIG. 2. FIG 3.

ANGULATION OF FORE LIMB.

FIG. 1. — *Elephas indicus*, longitudinal section of humerus, ulna and radius.
FIG. 2. — *Uintatherium cornutum*, longitudinal section of humerus, ulna and radius.
FIG. 3. — *Rhinoceros unicornis*, longitudinal section of humerus, ulna and radius.

In each humerus a line (*a–a*) is drawn through the central axis of the shaft and two lines (*b–b*) are drawn through the anterior and posterior intersecting edges of the proximal and distal articular surfaces or facets.

Several facts are at once brought out by these sections which bear upon the arthrology of the Ungulate limb.

(1) As the humerus, in the descent from the primitive bent-limbed types, is directly more vertically forwards, the articular facets are tilted from an oblique angle to more nearly a right angle with the shaft.

(2) At the same time the proximal or scapular facet shifts forwards, while the distal or ulno-radial facet shifts backwards upon the shaft's axis. An extreme instance of such shifting is shown in the transition from the rhinoceros (Fig. 3) to the elephant type (Fig. 1).

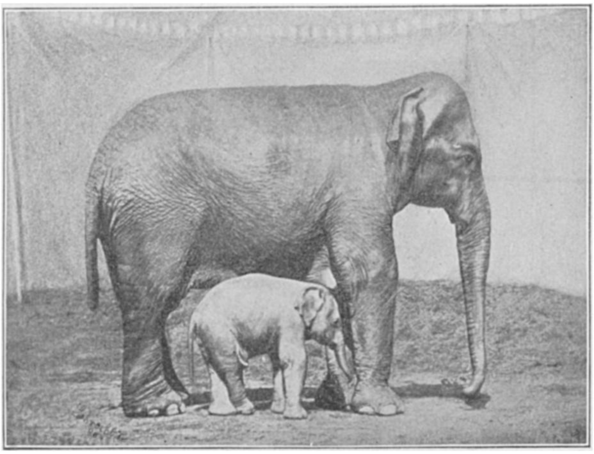

FIG. 4. — Mother elephant " Hebe " and baby " Americus," showing the excessive straightening or over extension of the fore limb. (By permission, from a copyrighted photograph by Schreiber & Sons, Philadelphia.)

(3) The proximal and distal articular facets shift uniformly, and their edges are always found to be in nearly parallel planes, *b–b*, *b–b*.

In the straight-limbed Proboscidia and Dinocerata, by this means the proximal articular facets of the humerus come to lie almost directly upon the top of the shaft. In the Dinocerata the articular facets are slightly more inclined to the axis of the shaft than in the Proboscidia. The difference, however, is only 4°, the elephant angle being 105°, while the Loxolophodon angle is 109°. This greater inclination is trifling when compared with the 130° of inclination seen in the rhinoceros, but it indicates that the humerus of Uintatherium was slightly more inclined and the elbow was slightly more bent than that of the elephant; the limb as a whole was therefore slightly more bent both in the standing position and in extreme extension.

The motions and positions of the elephant's limb, as shown by instantaneous photography, are very surprising. It is safe to say that the study of the skeleton alone would have given us a very faulty conception of this animal. The two most striking features are the great play of the wrist joint and the straightness of the limbs. Fig. 5 is an accurate tracing of a photograph of "Hebe," in a standing position, taken by Schreiber & Sons, of Philadelphia. The skeleton fore limb, reduced to the same scale, is sketched in, with as much flexure at the elbow joint as a fair allowance for the enveloping muscles will permit. It shows that, in standing, the bones of the fore limb are in a nearly vertical line from the scapula downwards. The elbow joint is, in fact, much straighter in extreme extension than we should have inferred experimentally by fitting the bones of the arm and fore arm together.

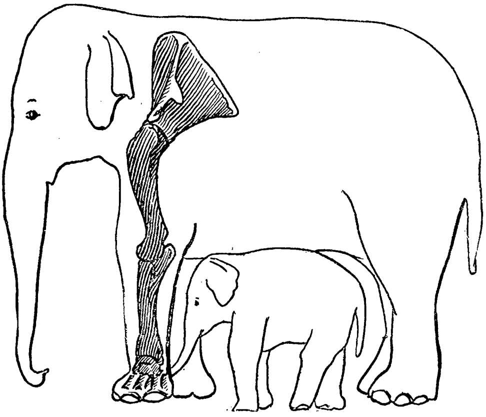

FIG. 5. — Diagram showing position of fore limb in "Hebe."

The conclusion is that the motions and positions of the limbs in the ponderous representatives of the most highly specialized Dinocerata were very similar to those of the modern elephants. The hind limb was as straight as in the elephant, and the fore limb in standing was a trifle more bent. A fore limb of Uintatherium in the Yale College collection gives evidence of considerable variation in this respect; some of the more primitive species, such as *Uintatherium mirabile*, were undoubtedly more straight limbed than others.

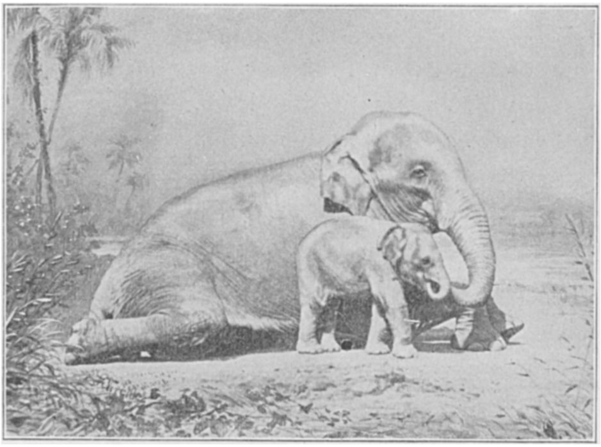

FIG. 6. — Same animal as in Fig. 4, showing sharp flexure at the wrist. (By permission, from a copyrighted photograph by Schreiber & Sons, Philadelphia.)

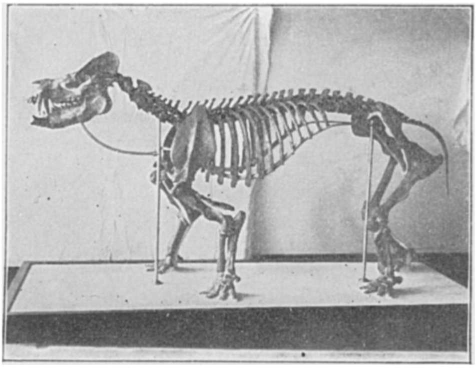

FIG. 7. — *Coryphodon testis*. Collection, American Museum of Natural History, showing marked primitive angulation of fore and hind limbs.

In the Coryphodontia of the lower Eocene, collateral ancestors of the Dinocerata, the angulation of the fore limbs is almost as great as that in the rhinoceros. In the still earlier forms, such as Pantolambda, of the basal Eocene, the angulation is almost equal to that in the Creodonta, from which this entire order sprang.

There is no doubt, therefore, that in my restoration of Loxolophodon, as well as in Professor Cope's restoration of the same animal, which was published later, the fore limb is somewhat too straight. On the other hand, Professor Marsh seems to have given the limb too much flexure in his restoration of *Uintatherium* (*Tinoceras*) *ingens*, a slightly older type than Loxolophodon.

The more vertical position of the limb is secondary, it is observed, in all large quadrupeds. In the Titanotheres it has not proceeded so far as in the above types of mammals. Among reptiles it is observed in the heavy quadrupedal Sauropoda.

The straightening of the limb is an adaptation designed to transmit the increasing weight through a vertical shaft. Correlated with it are the shifting of the facets into the direct line of pressure and the alteration of their planes from an oblique to a right or horizontal angle with relation to the vertical shaft.